PART III
INHERITANCE OF RESISTANCE TO DIFFERENT RACES OF *PIRICULARIA ORYZAE*[1]

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Introduction

Knowledge of genetics of blast disease resistance is important to rice breeders, but rather little has been accumulated. It is generally believed that rice varieties of the *indica* type are more resistant to the blast disease than the *japonica* varieties (Nakamori 1936, Hashioka 1950, Yamazaki 1959, Hsieh *et. al* 1961,1965). However, this is not consistent with the recent finding of physiological races. It seems not impossible that the resistance to different races of blast fungus be quite differently inherited and genes involved may differ too. Atkins (1965) found two independent genes each conditioning the reaction to a race. Basing on the degree of resistance to seven different races, Yamazaki and kiyosawa (1966) concluded that the dominancy of the resistance genes could vary according to environmental conditions.

The present study was conducted to find out genes controlling the resistances to different blast fungus races occuring in Taiwan, in order to obtain information of basic importance for the resistance breeding in rice.

Materials and methods

Both *japonica* and *indica* varieties of rice in current use by Chien (1963) as the differential hosts to identify physiological races of the blast fungus in Taiwan were mainly used as the cross parents. Some strains from U.S.A., Japan and other countries were also used. In order to avoid hybrid sterility, only such crosses as *japonica* x *japonica*, and *indica* x *indica*. were made. The F_2 plants between these strains grown in an experimental field were recorded for various segregating characters. Then, the F_2 plants and F_3 lines sown in plastic boxes (26x32x12 cm, filled with 6 kg of sandy loam soil and dressed with ammonium sulfate 3.5 gr., calcium superphosphate 2.5 gr., and potassium sulfate 1 gr.,) were tested for blast resistance. About 150 F_2 plants for each cross and 20-50 parental plants were planted side by side for comparison. They were top-dressed twice with 2% ammonium sulfate solution. For the first and second experiments, the materials were divided into two sets for inoculation with races 4 and 13. Inoculation was made at the five-leaf

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stage by spraying of spore suspensions onto the leaves and repeated 3-4 times so as to minimize the chance of escaping from infections. The flats were then placed in an inoculation chamber where the moisture (80-90%) and temperature (25-28°C) were controlled. Two days after inoculation the flats were moved out of the inoculation chamber and placed in a green house. The inoculated seedlings were examined and recorded with regard to the lesion types according to the following grading:

Grade	Degree of resistance	Lesion type	Description
O	HR	Immune	No visible sign of infection.
A	R	Brown spot	Small brownish-dark brown lesions or spots.
B	MR	Brown margin	Brownish lesions with a distinct border, which would not increase in size.
C	MS	Grayish white center	Slowly expanding lesions restricted in size.
D	S	Large lesions with dark green center	Large lesions surrounded by brownish bands.
E	HS	Large lesions with grayish center	Lesions are of water soaked appearance, often without well defined border, variable in size,and expanding rapidly.

Note: HR……Highly resistant　　R……Resistant
MR……Moderately resistant　　MS……Moderately susceptible
S……Susceptible　　HS……Highly susceptible

Types O, A and B were considered as resistant (R), while types C, D and E were considered as susceptible (S).

For the third experiment, inoculation was made by an injection methed, injecting spore suspension into the leaf sheath. One week after the injection, the degree of resistance was classified according to lesion types into resistant (R), medium (M) and susceptible (S) groups. The reaction M was considered resistant when the data were analysed. After recording the reaction to the first race, the leaves were clipped off and inoculation with the second race followed four to five days later.

Table 1. List of materials used in the experiment

Variety no.	Variety name	Reaction to races				Remarks
		4	13	22	25	
P109	Taipei 177	R	Sm			Ponlai variety (*japonica*)
P123	Taichung 65	R	S	Sm	S	〃
P130	Taichung 171	R	S	S	R	〃
P137	Kwanfu 401	R	S			〃
P140	Chianung 242	R	S	S	R	〃

P142	Chianan 3	R	S			〃
P151	Kaohsiung 27	R	S			〃
P162	Kwanfu 1	R	S	Sm	R	〃
P167	Pai-kan-tao	R	S	R	S	〃
P169	Chianung-yu 280	R	S	S	R	〃
P173	Taichung line 33	R	S	S	Rm	〃
P174	Taichung 184	R	R	R	R	〃
P175	Taichung 186	R	R	R	R	〃
J302	Nakamura	Rm	Sm			Japanese variety(*japonica*)
J306	Shinriki	R	Sm			〃
J313	Tamanishiki	S	R			〃
J317	Sensho	S	R	R	S	〃
J329	Kanto 51	S	R	R	R	〃
J331	Norin 21	Sm	R	R	R	〃
H25	Motzure-ine	S	R			Dwarf mutant (*japonica*)
H61		Sm	R	S	R	Gene marker from Japan
H106	Dwarf mutant (d_{42})	S	R			Dwarf mutant (*japonica*)
M506	Kung-shen-wu-shen-ken	S	S	R	S	Variety from China-main-land(*japonica*)
S256		S	R			*indica* variety
7102		Sm	Sm	S	S	Gene marker from U. S. A.
IG-65-2		R		Sm	Sm	Isogenic line of Taichung 65
IG-65-3		Rm	S	S	S	〃
C2180		R	R	S	S	Dwarf mutant d_{31}

Results

1.Reaction of F_2 seedlings to races 4 and 13

According to Chien (1963), race 4 was found most frequently in northern (Iran, Taipei) and central (Tungshu, Taichung) parts of Taiwan, while race 13 prevailed throughout the island. In the present study, more severe infection was generally seen when rice seedlings were sprayed with race 13 than with race 4. The infection types that these two races induced in the differential varieties were the same as that reported previously by Chien (1963) in majority of cases; however, in rare reactions in some varieties which are not consistent to the expectation were also observed.

1) Experiment I

The results of observations based on six disease lesion types as mentioned before, were further grouped into resistant and susceptible classes as given in Table 2. In the crosses of Taichung 65 x Norin 21, Taichung line 33 x Sensho, Taichung 171 x Sensho, Chianung 242 x Kanto 51, Chianung 242 x Sensho, the resistant and susceptible plants were segregated

into a 3:1 ratio showing that resistance to races 4 and 13 was each controlled by a single dominant gene.

In some of the crosses, reaction of only one race which gave mostly a 3:1 ratio was observed but reaction to other race was not observed due to the failure of second inoculation, such as Kwanfu 1 x Sensho, Kwanfu 1 x Kanto 51, Taichung 65 x Norin 21, Taichung 171 x Kung-shan-wu-shen-ken, etc. This shows that resistance to races 4 and 13 are each controlled by a single dominant gene which is similar to that reported by Atkins (1965) and Kiyosawa (1965).

Table 2. Reaction of F_2 seedlings to races 4 and 13 (Experiment 1)

Crosses	Races	Parental reactions	Resis-tant	Suscep-tible	Total	Segr. ratio	P
Taichung line 33 x Sensho	4	RxS	195	73	268	3:1	0.3-0.5
	13	SxR	102	36	236	3:1	0.7-0.8
Taichung 171 x Sensho	4	RxS	189	46	235	3:1	0.02-0.05
	13	SxR	129	39	168	3:1	0.5-0.7
Chianung 242 x Kanto 51	4	RxS	98	21	119	3:1	0.1-0.2
	13	SxR	101	20	121	3:1	0.02-0.05
Chianung 242 x Sensho	4	RxS	99	30	129	3:1	0.3-0.5
	13	SxR	74	48	122	3:1	<0.01
Taichung 65 x Norin 21	4	RxSm	42	18	60	3:1	0.3-0.5
	13	SxR	57	14	71	3:1	0.8-0.9
Pai-kan-tao x Kanto 51	13	SxR	77	21	98	3:1	0.3-0.5
Pai-kan-tao x Norin 21	4	RxSm	58	15	73	3:1	0.3-0.5
Kwanfu 1 x Sensho	4	RxS	91	27	118	3:1	0.3-0.5
Kwanfu 1 x Kanto 51	13	SxR	103	31	134	3:1	0.8-0.9
Taichung 171 x Kung-shan-wu- shen-ken	4	RxS	213	74	287	3:1	0.7-0.8
Chianung 242 x Norin 21	4	RxSm	74	28	102	3:1	0.5-0.7
Kwanfu 1 x Norin 21	4	RxSm	96	28	124	3:1	0.5-0.7
Kwanfu 1 x Kung-shan-wu- shen-ken	4	RxS	226	67	293	3:1	0.3-0.5

Table 3. Reaction of F_2 seedlings to races 4 and 13 (Experiment 2)

Crosses	Races	Parental reations	Resis-tant	Suscep-tible	Total	Segr. ratio	P
Tamanishiki x Shinriki	4	SxR	52	23	75	3:1	0.3-0.5
	13	RxSm	64	15	79	3:1	0.3-0.5
Tamanishiki x Kwanfu 401	4	SxR	65	22	87	3:1	0.9
	13	RxS	76	9	85	15:1	0.1-0.2
Shinriki x Sensho	4	RxS	44	29	73	3:1	<0.01
	13	SmxR	54	14	68	3:1	0.6-0.7
Chianan 8 x S 256	4	RxS	38	23	61	3:1	0.02-0.05
	13	SxR	38	19	57	3:1	0.2-0.3
Kaohsiung 27 x Tamanishiki	4	RxS	59	34	93	3:1	0.1-0.2
	13	RxSm	62	14	76	3:1	0.1-0.2
Pai-kan-tao x H 106	4	RxS	59	34	93	3:1	0.7-0.8
	13	SxR	62	14	76	3:1	0.05-0.01
Pai-kan-tao x Nagao H-25	4	RxS	38	18	56	3:1	0.3-0.5
	13	SxR	28	11	39	3:1	0.8-0.9
Taipei 177 x Tamanishiki	13	SmxR	46	22	68	3:1	0.9
Tamanishiki x Nakamura	13	RxSm	42	36	78	9:7	0.3-0.5
Sensho x Nakamura	4	SxR	39	29	68	3:1	<0.01

2) Experiment II

During 1965, different sets of F_2 materials were tested with races 4 and 13, in order to compare the results obtained in the first experiment. The spraying method was again employed for inoculation. The results are given in Table 3. As shown in Table 3, in the crosses of Tamanishiki x Shinriki, Pai-kan-tao x H106, Pai-kan-tao x H-25, Chianan 8 x S-256, a single gene segregation was found when inoculated with both races 4 and 13. This is similar to that of experiment I, showing that a single dominant gene controls resistance to respective race. However, cases of two genes controlling resistance to one race was also found as expressed by a 9:7 or 15:1 ratio. In some cases, the data are not fit too well to the expected ratio. This may be due to chance variation. The result of the second experiment is consistent with that of first experiment.

2. Relation between resistance gene Pi_4 and Pi_{13}

In order to know whether genes resistant to races 4 and 13 are linked or independent from each other, F_2 plants were first inoculated with race 4. After recording of disease reaction, the diseased leaves were clipped off and race 13 were inoculated. By this way, reaction of the same plants to different races can be compared. Strain C-2180 which carries dwarf gene d_{31} is resistant to both races 4 and 13, while purple leafed gene marker strain 7102 is moderately susceptible to both races 4 and 13. In the F_2 of C-1280×7102, single gene segregation indicated by a 3:1 ratio was seen when inoculated with both races. As shown in Table 4, the blast resistance gene named Pi_4 and Pi_{13} were found to be independent from each other after the chi-square test. Same is true in the cross of IG-65-2×7102 as shown in Tables 4 and 5.

Table 4. Seedling reaction of F_2 plants of C-2180 x 7102 to races 4 and 15

		Reaction to race 4			P for a 3:1 ratio
		R	S	Total	
Reaction to race 12	R	67	15	82	0.90-0.95
	S	20	7	27	
	Total	87	22	100	
P for a 3:1 ratio		0.20-0.30			

P for independence was 0.30-0.50

Table 5. Seedling reaction of F_2 plants of IG-65-2x 7102 to races 4 and 13

		Reaction to race 4			P for a 3:1 ratio
		R	S	Total	
Reaction to race 13	R	82	32	114	0.20-0.30
	S	38	9	47	
	Total	120	41	161	
P for a 3:1 ratio		0.80-0.90			

P for independence was 0.20-0.30.

Table 6. Reaction of F_2 Seedlings to races 22 and 25

Crosses	Races	Parental reactions	Resistant	Susceptible	Total	Segr. ratio	P
Chianung 242 x Norin 21	22	SxR	170	59	229	3:1	0.7-0.8
Sensho x Taichung 171	22	RxS	45	18	63	3:1	0.5-0.7

Sensho x Kung-shan-wu-shen-ken	22	RxS	117	28	145	3:1	0.1-0.2
Taichung 184 x Pai-kan-tao	25	RxS	166	51	217	3:1	0.5-0.7
Taichung 184 x Kung-shan-wu-shen-ken	25	RxS	217	65	282	3:1	0.3-0.5
Taichung 186 x Taichung 65	25	RxS	217	58	275	3:1	0.1-0.2
Taichung 186 x Pai-kan-tao	25	RxS	203	72	275	3:1	0.5-0.7
Sensho x Taichung line 33	25	SxR	180	66	246	3:1	0.5-0.7

3. Reaction of F_3 plants to races 22 and 25

As shown in Table 1, the parental strains Pai-kan-tao is resistant to race 22 and susceptible to race 25, Chianung-yu 280 is susceptible to race 22 and resistant to race 25. The reaction to the two races of their F_2 plants are in Table 7. The F_2 ratios both gave a good fit to the 3:1 ratio, indicating that the resistance to the two races were each controlled by a dominant gene. The data in the Table 7 show that the two genes controlling resistance to the two races are independent of each other. They are named Pi_{22} and Pi_{25} respectively. The F_2 plants between Chianung-yu 280 and Sensho also gave the same pattern of segregation as above as shown in Table 8.

Kun-shan-wu-shen-ken is resistant to race 22 but susceptible to race 25. In its cross with Chianung-yu 280, the F_2 ratios also gave a good fit to a 3:1 ratio. P for independence test between Pi_{22} and Pi_{25} was 0.30 to 0.50 showing no correlation between these two genes, as shown in Table 9. Taichung line 33 is highly susceptible to race 22, while Taichung 65 is moderately susceptible in this experiment. In the F_2 of cross between highly susceptible and moderately susceptible to race 22, the moderately resistant and susceptible plants were segregated into a 3:1 ratio. The independent relation between genes Pi_{22} and Pi_{25} was again found in the cross between Taichung line 33 x Taichung 65 as shown in Table 10. The same pattern of inheritance regarding the resistance to race 22 and 25 were found in the crosses of Taichung line 35 x Norin 21 and Taichung 171 x Taichung 65 as given in Tables 11 and 12.

Table 7. Seedling reaction of F_2 plants of Chianung-yu 280 x Pai-kan-tao to races 22 and 25

		Reaction to race 22			P for a 3:1 ratio
		R	S	Total	
Reaction to race 25	R	151	48	199	0.5-0.7
	S	47	15	62	
	Tatal	198	63	261	
P for a 3:1 ratio		0.70-0.80			

P for independence was 0.99-1.00

Table 8. Seedling reaction of F_2 plants of Chianung-yu 280 x Sensho to races 22 and 25

		Reaction to race 22			P for a 3:1 ratio
		R	S	Total	
Reaction to race 25	R	125	37	162	0.99-1.00
	S	39	15	54	
	Total	164	52	216	
P for a 3:1 ratio		0.70-0.80			

P for independence was 0.30-0.50

Table 9. Seedling reaction of F_2 plants of Chianung-yu 280 x Kung-shan-wu-shen-ken to races 22 and 25

		Reaction to race 22			P for a 3:1 ratio
		R	S	Total	
Reaction to race 25	R	150	40	190	0.80-0.90
	S	47	16	63	
	Total	197	56	253	
P for a 3:1 ratio		0.20-0.30			

P for independence was 0.30-0.50

Table 10. Seedling reaction of F_2 plants of Taichung line 33 x Taichung 65 to races 22 and 25

		Reaction to race 22			P for a 3:1 ratio
		R	S	Total	
Reaction to race 25	R	170	55	225	0.30-0.50
	S	55	12	67	
	Total	225	67	292	
P for a 3:1 ratio		0.30-0.50			

P for independence was 0.20-0.30

Table 11. Seedling reaction of F_2 plants of Taichung line 33 x Norin 21 to races 22 and 25

		Reaction to race 22			P for a 3:1 ratio
		R	S	Total	
Reaction to race 25	R	158	48	206	0.50-0.70
	S	51	24	75	
	Total	209	72	281	
P for a 3:1 ratio		0.70-0.80			

P for independence was 0.10-0.20

Table 12. Seedling reaction of F_2 plants of Taichung 171 x Taichung 65 to races 22 and 25

		Reaction to race 22			P for a 3:1 ratio
		R	S	Total	
Reaction to race 25	R	151	40	191	0.10-0.20
	S	36	14	50	
	Total	187	54	241	
P for a 3:1 ratio		0.30-0.50			

P for independence was 0.20-0.30

4. Reaction of F_3 plants to races 4 and 22

Pai-kan-tao is highly resistant to race 4, while H-61 is susceptible. The F_3 lines of their hybrid could be divided into resistant, segregating and susceptible classes, giving a good fit to the 1:2:1 ratio (Table 13). Same is true in the crosses of IG-65-2 x P167 and IG-65-3 x P167. Presence or absence of linkage between Pi_4 and Pi_{22} was not tested owing to a failure of inoculation with race 22.

Table 13. Reaction of F_3 seedlings to races 4 and 22

Cross	race	Observed no. of lines				Expected ratio	X^2	P
		R	Seg.	S	Total			
P167		9						
P167xH-61	4	70	136	64	270	1:2:1	0.2815	0.8-0.9
H-61				10				

IG-65-2				14				
IG-65-2xP167	22	52	119	57	228	1:2:1	0.6529	0.7-0.8
P167		12						
IG-65-3				14				
IG-65-3xP167	22	73	140	60	281	1:2:1	0.1815	0.9-0.95
P167		12						

5. Genotypes of blast resistance in parental varieties

The segregation ratios of resistance to races 4 and 13, 22 and 25 in the above mentioned experiment are summarized in Tables 14 and 15. The blank in these tables still needed to be filled out by the further test. The genotypes for resistance genes of the ten parental strains may then be presumed as follows:

Pai-kan-tao ·····Pi_4; pi_{13}; Pi_{22}; pi_{25}
Sensho ·····Pi_{13}; Pi_{22}
Chianung-yu 280. ···Pi_4; pi_{22}; Pi_{25}
IG-65-2 ·····Pi_4; pi_{13}; pi_{22}
IG-65-3 ·····Pi_4; pi_{13}; pi_{22}
H-106·····pi_4
C-2180 ·····Pi_4; Pi_{13}
Taichung line 33·····Pi_4; pi_{22}; Pi_{25}
Taichung 65 ·····pi_{22}; pi_{25}
Kanto 51 ·····pi_4; Pi_{13}; Pi_{22}; Pi_{25}

Varieties identified to carry blast resistance genes Pi_4, Pi_{13}, Pi_{22} and Pi_{25} are given in Table 16.

Table 14. Segregation ratios of resistance and susceptible to races 4 and 13 of *Piricularia Oryzae*

	Kanto 51		Pai-kan-tao		Tamanishiki		Sensho		S-256	
	race 4	race 13	race 4	race 13	race 4	race 13	race 4	race 13	race 4	race 13
Kwanfu 1		3:1					3:1			
Kwanfu 401	3:1	3:1			3:1	15:1				
Chianung 242							3:1	3:1		
Chianung-yu 280			3:1				3:1			
Chianan 8					3:1	3:1			3:1	3:1
Kaohsiung 27					3:1	3:1				
Taichung line 33							3:1	3:1		
Taichung 171							3:1	3:1		
IG-65-2			3:1							
IG-65-3			3:1							

Shinriki	3:1				3:1	3:1	3:1	3:1		
Nakamura						9:7	3:1			
Kanto 51				3:1						
Norin 21			3:1							
H-25			3:1	3:1						
H-106			3:1	3:1						

Table 15. Segregation ratio of resistance and susceptible to races 22 and 25

	Taichung 65		Taichung 184	Taichung 186	Chianung-yu 280		Sensho		Norin 21	
	race 22	race 25	race 25	race 25	race 22	race 25	race 22	race 25	race 22	race 25
Pai-kan-tao	3:1	3:1	3:1	3:1	3:1	3:1		3:1		
Taichung line 33	3:1	3:1						3:1	3:1	3:1
Taichung 171	3:1	3:1					3:1	3:1		
Taichung 186		3:1								
Kung-shan-wu-shen-ken	3:1	3:1	3:1	3:1	3:1	3:1	3:1			
Sensho					3:1	3:1			3:1	3:1

Table 16. Varieties identified to carry blast resistance genes Pi_4, Pi_{13}, Pi_{22}, Pi_{25}

Blast resistance genes	Variety name
Pi_4	Taichung 65, Taichung 171, Taichung lines 33, Kwanfu 1, Kwanfu 401, Chianan 8, Chianung 242, Kaohsiung 27, Nakamura, Shinriki, Pai-kan-tao, C-2180.
Pi_{13}	Taichung 171, Taichung 184, Taichung 186, IG-65-2, Tamanishiki, Sensho Kanto 51, Norin 21, H-106, C-2180
Pi_{22}	Pai-kan-tao, Kanto 51, Norin 21
Pi_{25}	Taichung 171, Taichung 184, Taichung 186, Taichung line 33, Kwanfu 1, Kanto 51, Chianung-yu 280

6. Relation between leaf- and neck-blast resistances

How the resistance of leaf and that of panicle neck are correlated has been a problem of general interest. As shown in Table 17, 81% of strains tested showed positive correlations between leaf and neck blast resistances, while the remaining 19% showed no correlations. Question then arises as to whether or not the leaf and neck blast resistances are controlled by the same genes. Hashioka (1950) reported that some varieties, the number of the infected ears, has no correlation with the susceptibility of the leaves. The writer (Hsieh 1965) estimated phenotypic and genetic correlations between leaf and neck blast resistances in F_2 populations. He found that though phenotypic correlations differed according to crosses, genetic correlations were in most crosses high (rg=0.3-0.9). This suggests that the same genes control both leaf and neck resistances. The reason for the absence of the cor-

relation in certain crosses seems to need further investigations.

Table 17. Number of strains classified according to leaf-and neck-blast resistances

Relation between leaf and neck blast resistances	Locations							
	Taipei	Taichung	Chiayi	Kaohsiung	Taichung	Total	%	
L. N.	65	29	60	73	39	265	43.5	81
l. n.	38	68	37	35	50	228	37.5	
L. n.	9	28	4	10	10	61	10.0	19
l. N.	12	0	23	6	14	55	9.0	

Note: L.N.·····Resistant to both leaf and neck blasts
l. n.·····Susceptible to both leaf and neck blasts
L. n.·····Resistant to leaf blast but susceptible to neck blast
l. N·····Susceptible to leaf blast but resistant to neck blast

7. Test of linkage between Pi_4, Pi_{22} and other maker genes

One of the parental strain H-61 carries C^{BP}, *A p* for apiculus coloration. *Bf* for brown or dark furrows and d_2 for its dwarf stature. Pai-kan-tao has *C a P* ps_1 ps_2 *Bf* for the above characters and ligulelessness gene *lg*. From the cross of these two strains, Pi_4 as well as Pi_{22} were found to be independent of all the above mentioned genes. In the cross of pai-kan- tao with IG-65-2 or IG-65-3 carrying the phenol reaction gene, *Ph* and/or a red pericarp genes *Rc*, *Rd*, Pi_{22} was found to be independent of *Ph* and *Rc*.

Table 18. Test of independence between blast resistance genes and those for other characters

Crosses	Blast resistance genes	Marker genes	Combined characters					P
			AB	Ab	aB	ab	Total	
P167× H-61	Pi_4	*A*;*P*(Apiculus color)	110	96	35	29	270	0.80-0.90
P167× H-61	Pi_4	Ps_1;Ps_2 (Stigma color)	41	69	13	32	145	0.99-1.00
P167× H-61	Pi_4	*Bf*; I-Bf (Brown furrow for lemma and palea)	23	86	6	30	145	0.50-0.70
P167× H-61	Pi_4	d_2 (Ebisu dwarf)	155	51	51	13	270	0.30-0.50
IG-65-2× P167	Pi_{22}	*Rc*	115	56	40	17	228	0.50-0.70
IG-65-2× P167	Pi_{22}	*Ph* (Phenol reaction)	133	37	47	9	226	0.30-0.50
IG-65-3× P167	Pi_{22}	*Ph*	153	60	49	18	281	0.80-0.90

Table 19. Test of independence between ligulelessness gene *lg* and blast resistance genes.

Crosses	Blast resistance genes	Ligulelessness genes	Combined characters					P
			AB	Ab	aB	ab	Total	
P167×H-61	P_4	*lg*	143	58	46	18	270	0.99–1.00
P167×J331	Pi_4	*lg*	36	13	16	5	70	0.99
P167×P123	Pi_{13}	*lg*	121	23	40	13	197	0.10–0.20
P167×J331	Pi_{13}	*lg*	29	11	33	4	77	0.30–0.50
P167×J329	Pi_{13}	*lg*	51	21	16	5	93	0.95–0.98
IG-65-2×P167	Pi_{22}	*lg*	138	33	49	8	223	0.30–0.50
IG-65-3×P167	Pi_{22}	*lg*	164	49	57	11	281	0.20–0.30
P169×P167	Pi_{22}	*lg*	148	50	45	18	261	0.50–0.70
P169×P167	Pi_{25}	*lg*	148	53	48	16	265	0.80–0.90
P174×P167	Pi_{25}	*lg*	124	42	37	14	217	0.70–0.80

In our previous experiment using natural infection (Hsieh *et. al.* 1965), *lg* was linked with an unidentified resistance gene. Also by natural infection, Oka and Lin (1957), reported a linkage between *Ph* and a resistance gene. In view of the above results of linkage test, Pi_4,Pi_{13},Pi_{22} and Pi_{25} may not be synonymous with these unidentified resistant genes.

8.Test of breeding materials with different races of blast fungus

In the light of recent findings on pathogenic races of the blast fungus, breeders in Taiwan are realizing the importance to take this problems into consideration. Test of the breeding materials with races of the fungus were made as the first step in this direction. 50 strains from Taiwan, Japan, U.S.A., India and philippines were tested with 27 races of the blast fungus. Races 12, 13 and 16 are of the most pathogenic ones among the 27. There was a trend for most introduced varieties, either *japonica* or *indica* type, to show resistant reaction to a majority of the races tested. In contrast, varieties which have long been grown in Taiwan showed a wide range of variation in the susceptibility to Taiwanese races. This may be of interest to notice.

In Table 20. The varieties were classified according to the number of races to which they showed resistance.

As shown in Table 18, Taipei 306, Taipei 308, and Kaohsiung 24 were resistant to only one of eight races tested. The U.S. variety Caloro was resistant to only two of ten races. Japanese varieties Pi no. 1, Ginga, Homare-nishiki showed resistances to 9 races, while Chokoto, Yakeiko, Ishikarishiroke were resistant to all the 10 races tested. Zenith, Rexaro (from U.S.A.), Tadukan, Dular (from India), Wag-wag (from Philippines) also showed resistances to all the 10 races tested. Taichung 65 a representative of Ponlai variety in Taiwan was resistant to 10 races but was susceptible to 17 races. Taichung native 1 (*indica*), showed resistance to 7 of 8 races tested.

Taichung line 33, Chianung-yu 280, Norin 21 and Kanto 51 were the most resistant ones showing resistances to 18 of 27 races tested. The more resistant genes a variety carries, the more it would be desirable. Such varieties may be obtained by combining many resistance genes by hybridization. Varieties carrying many blast resistance genes, such as Taichung lines 33, Kanto 51, Norin 21, Chianung-yu 280 and Pai-kan-tao, may be used as the cross parents.

Even though gathering of all resistant genes in a veriety is not possible, it is not difficult to combine in a variety, genes controlling the resistance to two or three races predominating in a region.

Table 20. Varieties grouped according to the resistance to different races of the blast fungus

Number of races of which resistance is found	Variety name
1	Taipei 306*, Taipei 308*, Kaohsiung 24*,
2	Taipei 177*, Hsinchu 56*, Tainan 1*, Chianan 8*, Kaohsiung10*, Kaohsiung 27*, Kaohsiung 64*, Kaohsiung 122*, Tainan 1*, Caloro**
3	Taichung 178*
4	Tainan 3*
5	Hsinchu 61*, Ai-chio-chien*, Natala
6	Norin 20*, Aichi-asahi*
7	Taichung native 1*, Kung-shan-wu-shen-ken
8	Taichung 184*, Taichung 185*, Norin 22*, Lacrose**
9	Pi no. 1*, Ginga**, Homare-nishiki**
10	Taichung 65, Chokoto**, Yakeiko**, Ishikari-shireke**
11	Zenith**, Rexaro**, Tadukan**, Wag-wag**, Dular**, Raminad Str. 3**, CI 5309**
12	Taichung-ti-chio-wu-chien
13	Kao-chio-liu-chao, Kaohsiung-ta-li-chen-yu
14	Chianung 242, Cutsugucul
15	Kwang-fu 1
16	Sensho
17	Taichung 171, Pai-kan-tao
18	Taichung line 33, Chianung-yu 280, Norin 21, Kanto 51.

Note:
1. *...Tested with eight races i. e. nos. 1,5,12,13,16,17,24 and 26.
2. **...Tested with ten races i. e. nos. 3,5,11,13,14,16,17,22 and 26.
3. .....Unmarked ones were tested with all 27 races.

Discussion

As mentioned in the introduction, recent genetic studies of blast diseases resistance using identified fungus races proved that the resistance to a particular race was controlled by a dominant gene (Atkins 1965, Kiyosawa 1965). The results we obtained in this study

are consistent with this. We found the four resistance genes Pi_4, Pi_{13}, Pi_{22} and Pi_{25}, which seemed to be independent of one another in some cases. The above-named workers also reported independency of resistance genes they found. A number of genes controlling resistance to different fungus races might be distributed in different chromosomes. If more linkage experiments are made, their linkage relations with marker genes may be worked out.

It seems that when a particular fungus races is used in an experimental condition, the "gene-to-gene" hypothesis of Flor (1955) generally applies. Segregation of two or more genes reported by earlier workers Nakamori 1936; Hashioka 1950; Yamazaki 1959; Hsieh *et. al.* 1961, 1965 might be due to the use of a mixture of different races or natural infection. However, breeders experience that "field resistance" can not always be explained well by the results of controlled experiments, How the resistance genes work in different genetic backgrounds and in different environments needs further investigation.

It is concluded that blast resistance is simply inherited character. Resistance of a variety to different races is due primarily to a single gene though it is possible minor or modifying genes also influence to degree of resistance. More experiments are to be made in the future to look into this problem.

Summary

1) The F_2 and F_3 hybrids between 28 *japonica* rice strains were tested for blast disease resistance by using four different races, 4, 13, 22 and 25. Spore suspension was inoculated with rice seedlings at the five-leaf stage by using both spraying and injection methods.

2) The resistance to the four races were found to be each controlled by a resistant gene. The four resistance genes found, Pi_4, Pi_{13}, Pi_{22} and Pi_{25} were independent of one another in some cases. Also they were not linked with marker genes involved in the crosses, *A,P, Ps, lg, Bf, I-Bf,* d_2, *Rc* and *Ph.*

3) The resistances to leaf and neck blasts widely varied due to variety, year, crop season and location. In 81% of strains so far tested, leaf and neck resistances were correlated, and appeared to be controlled by the same genes. In the remaining 19%, the leaf and neck resistances were not correlated. Whether or not this is due to the occurrence of different races remains unknown.

4) 50 rice strains from Taiwan, Japan, U.S.A., India and Philippines were tested with the 27 races of blast fungus. Races 12, 13 and 16 are the most pathogenic ones among them. Newly introduced varieties, either *japonica* or *indica* type, tended to be resistant to a majority of the races tested. Taichung line 33, Chiauung-yu 280, Norin 21 and Kanto 51 were the most resistant ones, showing resistances to 18 of the 27 races tested. These varieties were considered to be desirable materials for the blast resistance breeding program in Taiwan.

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NEED FOR ADDITIONAL RESEARCH

Future plan of breeding for resistant varieties

1) Breeding of varieties having more than two major resistant genes.

As the data in the present studies show, Taipei 306, Taipei 308, and kaohsiung 24 are resistant only to race 1. They are presumed to carry one resistant gene, Pi_1. If other races than no. 1 predominant, these varieties may lose their resistance. Varieties with two or more resistant genes, may not lose resistance so easily. Such varieties must be established. In practice, however, the more the resistance genes to be combined, the more difficult would be the work, and some resistant genes may be linked with other genes controlling undesirable

characters. Cross parents may be selected from varieties listed in Table 20.

2) Breeding of isogenic lines each carrying a major resistance gene.

Breeding of varieties carrying a major gene is relatively easy. Varieties adaptive to different regions may be used as the recurrent parents of back-crosses for obtaining isogenic lines with certain resistant genes. Tsai and Oka (1965) developed isogenic lines of Taichung 65 carrying genes for early maturity, positive phenol reaction, glutinous endosperm etc, by back-crossing. Since the degree of blast resistance of a strain widely varies due to locations and yeârs, environmental modifications must be carefully observed for performing this work. If many isogenic lines become available, a few selections of them may be grown according to the fungus races predominating in a given region. Recording and forecasting of prevalent races should be made every year in each locality. pathogenic mutations of the races if frequently may make this effort fruitless, however.

3) Mixture of various isogenic lines to make up a variety

Various isogenic lines of the same variety may be mixed to form a "multi-line". The variety, kind and number of isogenic lines to be mixed must be determined according to the prevalent races in a given region. Such a "multi-line" veriety may be usefull especially when various races spontaneously occurred in a region. Though the breeding of many isogenic lines needs a long time and much labor, this may be attempted in the future.

4) Application of field resistance

Varieties truely resistance to a race or races are not always completely resistant in the field where the given race or races prevail. The mechanism of "field resistance" seems to remain unknown. Minor genes may possibly be concerned. It is important to select field resistance together with true resistance. It seems that a breeding program should be conducted under both controlled and natural conditions.